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IDENTITY OF THE OAK TREE AT LIVE OAK TANKS, JOSHUA TREE NATIONAL MONUMENT, CALIFORNIA

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Oaks are no rarity in Joshua Tree National Monument. The desert scrub oak, *Quercus turbinella* Greene ssp. *californica* Tucker, a shrub or small shrubby tree, is quite common and locally abundant. Two other species, *Q. dunnii* Kell. (*Q. palmeri* Engelm.) and *Q. chrysolepis* Liebm., also are found in the Monument, although at only a few locations (Adams, 1957). The former is a shrub; the latter also may be a shrub, but more commonly is arborescent. In the entire Monument, however, there is only one oak tree of any size—a symmetrical 30-foot tree (fig. 1) at Live Oak Tank (fig. 2).

The identity of this tree has long been a matter of conjecture and disagreement among Californian botanists. It is a white oak (a member of the subgenus *Lepidobalanus*), but clearly is not referable to any species recorded for California. This, plus the fact that it is a single, isolated individual of its kind, raises the possibility of its being a hybrid of some sort. In size, degree of lobing, and dentation of lobes, the leaves are very similar to certain hybrids between species with small, spinose- or mucronate-dentate leaves (as one parent), and species with moderately large, deeply lobed leaves (as the other parent); *Q. turbinella* × *Q. gambelii* (Tucker, 1961), and *Q. dumosa* × *Q. garryana* (Tucker, 1953) come to mind. The leaves of the suspected hybrid have mucronate lobes and teeth. Logically, one parent could have smaller leaves with spinose-dentate margins. This suggests *Q. turbinella californica,* which occurs with the putative hybrid at Live Oak Tank. As for the other parent, it should logically be another white oak, for no authentic case is thus far known of natural hybridization between different subgenera. If we attempt to extrapolate the characters of the other parent in the manner of Anderson (1949), the detailed reasoning of such an analysis would be that presented in Table I.

TABLE I. EXTRAPOLATION OF THE CHARACTERS OF THE SECOND PARENTAL SPECIES OF THE PUTATIVE HYBRID.

Since *Q. turbinella californica* has (is):	but the putative hybrid has (is):	the probable second parent has (is):
Characteristically a shrub	A fair-sized tree	A large, or moderately large tree
Small leaves (commonly 15-35 mm long) with very short petioles	Larger leaves (40–60 mm long) with longer petioles	Even larger leaves (over 60 mm long) with longer petioles
Dentate margins with spinose teeth	Moderately lobed leaves, the lobes mucronate	Deeply lobed leaves with rounded or, at most, obtusely pointed lobes
Grayish-green upper leaf surfaces	Moderate green to yellow-green upper surfaces	Dark green upper surfaces
Thin acorn cups that are scarcely, or not at all, tuberculate, and are turbinate to sub-hemispheric in shape	Thicker cups that are moderately tuberculate, and are hemispheric in shape	Thick, strongly tuberculate cups, that are hemispheric to deeply bowl-shaped
Nuts that are commonly on the order of 20–25 mm in length	Nuts that are mostly 30–35 mm in length	Nuts 40 mm or more in length

In all the western states only one species fits such a description—*Quercus lobata*. The leaves, acorns, and cups of the hybrid are compared with those of the putative parents in Figs. 3, 4, and 5, respectively. The nearest trees of *Q. lobata,* however, are approximately 150 miles to the northwest, along the south side of Antelope Valley in northwestern Los Angeles Co. This poses an obvious problem, which will be discussed later.

In addition to the characters listed in Table I, other significant but less obvious features of the hybrid could be mentioned: 1, the canescence of the acorn cups is very similar to that in *Q. lobata,* and 2, the stellate hairs of the lower leaf surface are intermediate, most clearly in the size of the lumen of the individual rays (fig. 6).

Another character in which the putative parents differ is the degree of leaf persistence. In *Q. turbinella californica* the leaves ordinarily persist through the winter. In *Q. lobata* they are completely deciduous, dropping in the fall or early winter. The hybrid is clearly evergreen and is thus more similar to *Q. turbinella* in this respect. (James R. Youse and Alan D. Eliason of the Monument staff kindly made observations on this character for me.) Aside from this one conspicuous physiological trait, therefore, the oak at Live Oak Tank is essentially intermediate between the two postulated parental species.

I take pleasure in naming this distinctive hybrid for Philip A. Munz, who in years past has shown considerable interest in its identity.

Quercus × **munzii** Tucker, hybr. nov. *Q. lobata* Née × *Q. turbinella* ssp. *californica* Tucker. Arbor ca. 9 m alta; ramuli diametro 1.5–2.5 mm griseo- vel brunneo-bubalini, plus minusve tomentosi; gemmae ovoideae,

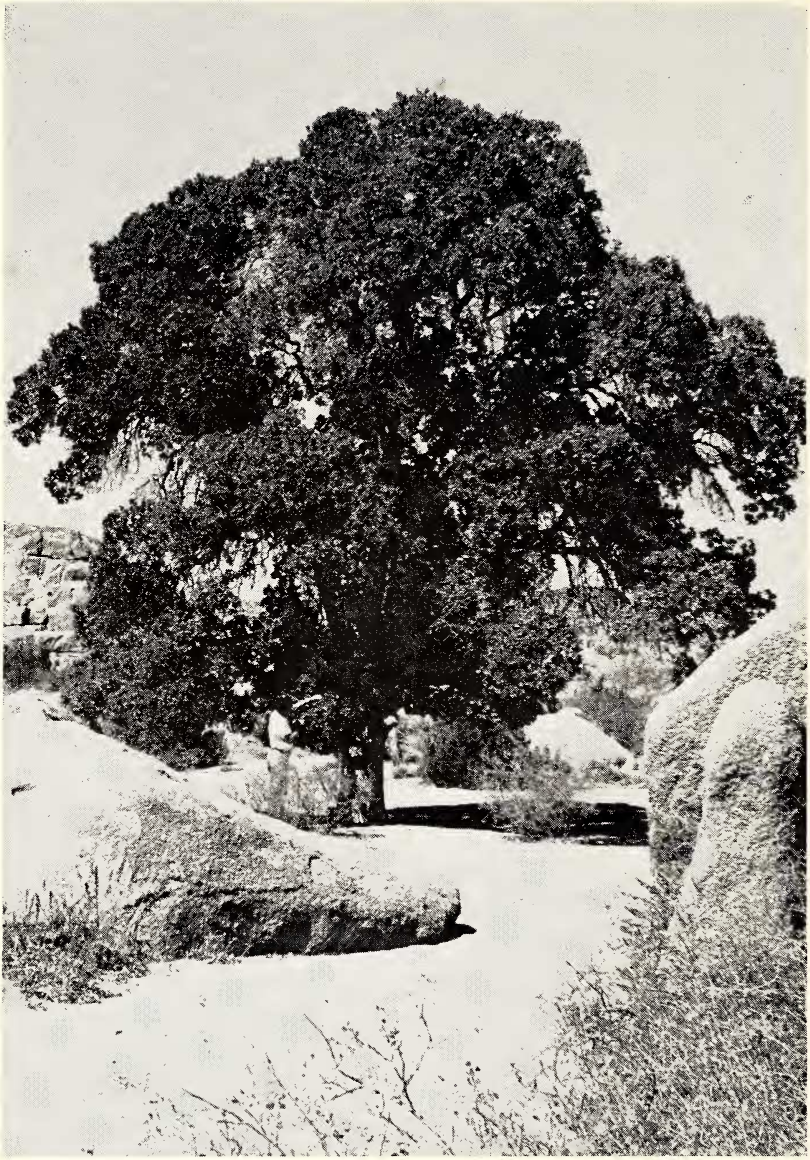

Fig. 1. The hybrid oak, *Quercus* × *munzii (Q. lobata* × *Q. turbinella* ssp. *californica)* at Live Oak Tank, Joshua Tree National Monument, Riverside Co., California.

sparse adpresso-pubescentes vere vel laeve brunneae, 2.5–4 mm longae; folia sempervirentia, 4–6 cm longa, 1.5–3.5 cm lata, ambitu obovata, basi late cuneata vel rotundata vel subtruncata, saepe inaequalia margine irruglariter leviterque lobata, supra vere vel luteovirdia, stellato-pu-

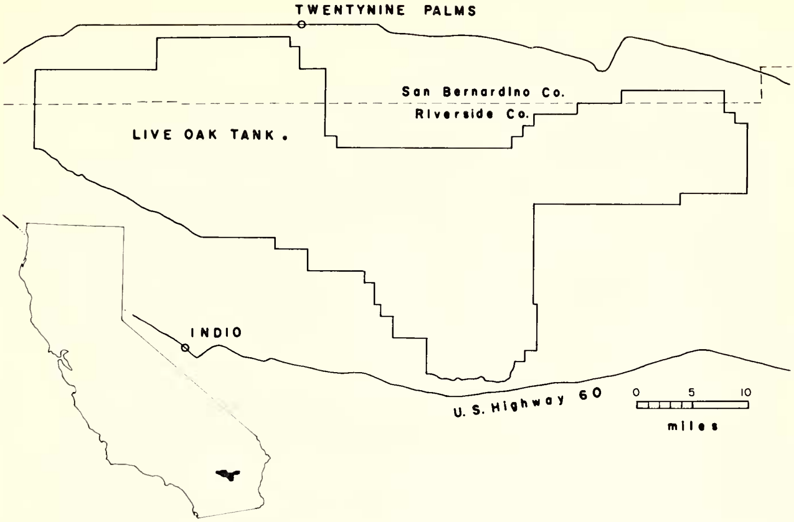

FIG 2.. Joshua Tree National Monument, showing Live Oak Tank, the location of the hybrid.

berulenta, subtus pallide viridia hebitiaque, dense sed minute adpresse stellato-puberulenta, lobis terminaliter 2-pluritaliter mucronate brevidentatis, venis utrinsecus 3–5; petioli puberulenti 5–8 mm longi; fructus annuus, cupula hemisphaerica, 13–19 mm lata, 6–9 mm alta, squamae plus minusve tuberculatae pallide brunneo-griseae, canescentes, apice sparsissime canescentes ac pallide brunneae; glans ovoidea demum atrobrunnea glabrataque, 30–35 mm longa, 12–17 mm lata.

Thee ca. 9 m tall with round, symmetrical crown; trunk ca. 7.5 dm in diameter at 6 dm above ground. Trunk bark light brownish-gray, flaky, rather soft and corky. Twigs of the current year's growth 1.5–2.5 mm in diameter, grayish- or brownish-buff, moderately tomentose, with small, inconspicuous, light-colored lenticels. Buds 2.5–4 mm long, ovoid, sparsely appressed-pubescent, medium to light brown in color. Stipules not seen. Leaves evergreen, obovate (sometimes narrowly so) in outline, 4–6 (or 8) cm long, 1.5–3.5 (4) cm broad, base broadly cuneate to rounded or sub-truncate, often unequal, margin irregularly and shallowly lobed, the lobes 2- several-toothed, the lobes or teeth mucronate; upper surface medium to yellow-green, stellate-puberulent, lower surface pale green and dull, densely but minutely appressed stellate-puberulent; principal secondary veins 3–5 on a side; petioles 5–8 mm long, puberulent. Staminate catkins 2 cm or more long, rachis tomentulose, perianth glabrate, the margins of the narrow lobes irregularly fimbriate, the small, glabrous, oval anthers slightly exserted. Fruit annual; acorn cups hemispheric to bowl-shaped, 13–19 mm broad, 6–9 mm high, scales deltoid, tips of the upper ones tending to be ligulate, bases of the scales moderately tuberculate, light brownish-gray, canescent, the tips sparsely so and

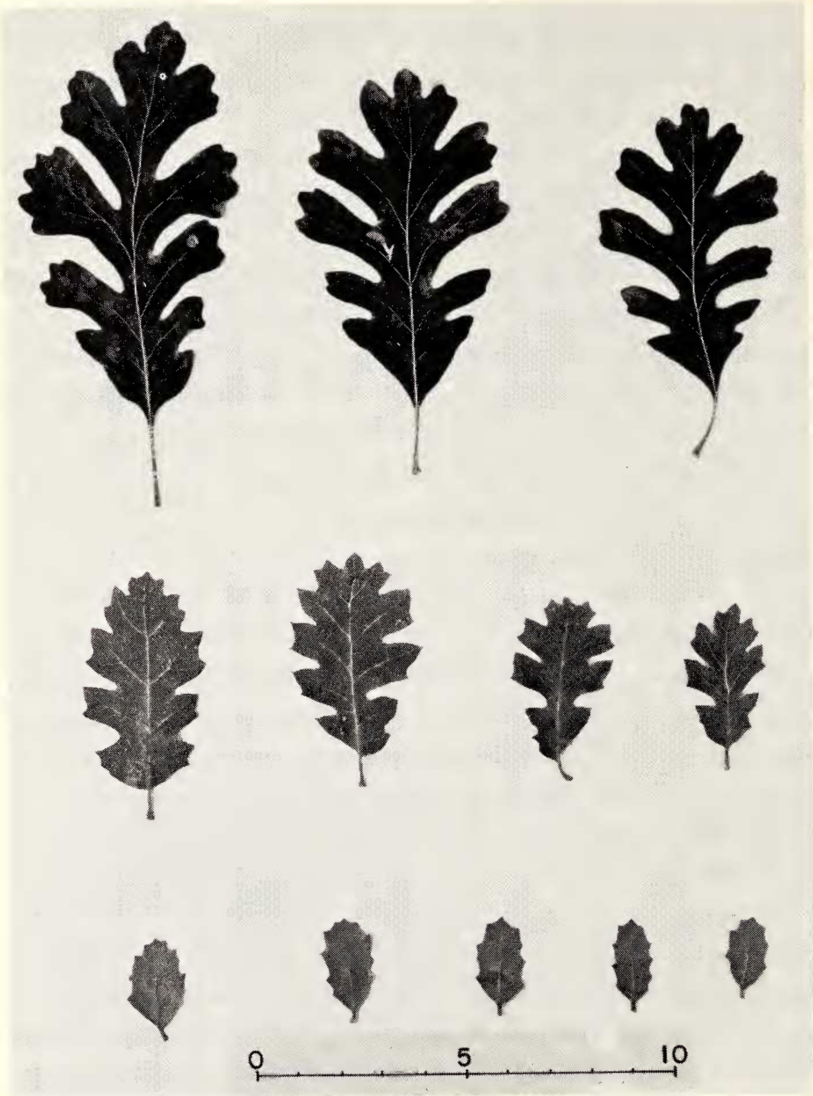

FIG. 3. Leaves of *Quercus* × *munzii* (middle row: *Tucker 3886* and *Cavagnaro*). *Q. lobata* (top row: *Tucker 3905*), and *Q. turbinella* ssp. *californica* (bottom row: *Tucker 3895* and *Cavagnaro*). Scale is in cm.

medium brown in color; acorn ovoid, 30–35 mm long, and 12–17 mm broad, dark brown at maturity, glabrate except for the minutely canescent apex.

Specimens examined. Live Oak Tank, 4,000 feet, Joshua Tree National Monument, Riverside Co., California: *Tucker 3886* and *Cavagnaro* (holotype-DAV), Oct. 2, 1965; *Bowerman 4100; Munz 11590* (RSA);

FIG. 4. Acorns of *Quercus* × *munzii* (middle row: *Tucker 3886* and *Cavagnaro*), *Q. lobata* (top row: *Tucker 3905*), and *Q. turbinella* ssp. *californica* (bottom row: *Tucker 3895* and *Cavagnaro*). Scale is in cm.

Eliason and *Youse s. n.* (DAV), Jan. 17, 1966; *Eliason s. n.* (DAV), June 12, 1966.

The parental species are, for the most part, well-separated ecologically. *Quercus turbinella californica* is the shrubby, gray-leaved oak of the pinyon-juniper association along the western edge of the Mojave Desert,

FIG. 5. Acorn cups of *Quercus* × *munzii* (middle: *Tucker 3886* and *Cavagnaro*), *Q. lobata* (left: *Tucker 3905*), and *Q. turbinella* ssp. *californica* (right: *Tucker 3895* and *Cavagnaro*). Scale is in cm.

and of the xeric chaparral in the more arid parts of the inner South Coast Ranges. *Quercus lobata* is the most characteristic tree of interior valleys in California. Old trees with massive trunks and enormously broad, rounded crowns are a familiar sight in many interior parts of the state. In some areas, however, the two species may occur in close proximity to one another. For example, *Q. lobata* occurs along U. S. Highway 99 about 2 miles northwest of Lebec, Kern Co., and *Q. turbinella californica* is abundant on the adjacent hillsides. They also occur together along Oak Creek, 14 miles west of Mojave, Kern Co., on the desert slopes of the Tehachapi Mountains. The tree at Live Oak Tank, however, is the only hybrid between them known to me.

The botanist concerned with experimentally testing a hypothesis of hybridity, may either (1) attempt to synthesize the hybrid by crossing the putative parents, or (2) make a progeny test, if seeds are available from the putative hybrid. In the latter procedure, if the seedlings segregate morphologically such that some of them resemble one putative parent and some the other, the hypothesis is confirmed.

To the best of my knowledge, no attempt has yet been made to cross the putative parents of *Q.* × *munzii*. Progeny tests, however, have been attempted at least twice. In Oct., 1946, Munz collected acorns from this tree. From these, 105 seedlings were eventually planted at the Rancho Santa Ana Botanic Garden (Percy Everett, pers. commun.). Munz observed subsequently that the young oaks differed markedly from one another. "Some began to grow fast and upright like young trees, others branched at the base and were shorter and more bushy; some were more deciduous than others" (Vanderspek, pers. commun.). Everett stated, however, that only one small plant was still alive at the date of his writing in 1963. On Nov. 22, 1956, ten years after Munz's collection, acorns were collected from the hybrid by Ralph D. Cornell (Landscape Architect, Los Angeles), and seedlings from these were planted at the Garden Oct. 17, 1957, according to Everett. Specimens were collected for me from the 11 plants still surviving in 1963. These were all more *turbinella*-like than the parent tree, having generally smaller and more conspicuously spinose leaves than the latter. Thus, they probably represented backcrosses to *Q. turbinella californica* which, as stated previously,

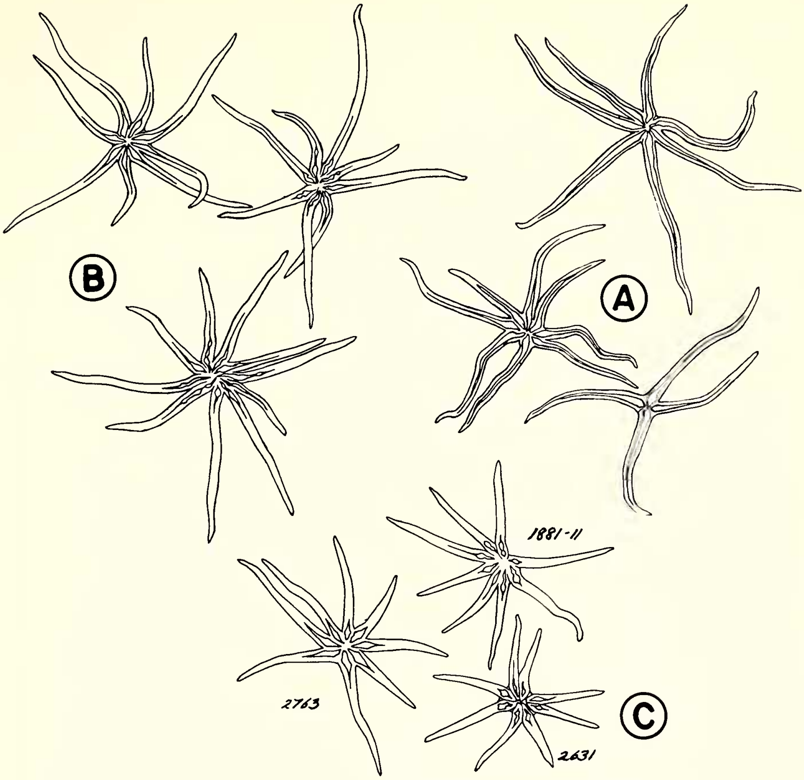

FIG. 6. Representative stellate hairs of the lower leaf surface of (B) *Quercus* × *munzii (Munz 11590),* (A) *Q. lobata (Tucker 3442),* and (C) *Q. turbinella* ssp. *californica (Tucker 1881–11, 2631, 2763)*. Drawings by Miss Jean Addicott; all × ca. 50.

occurs in the immediate vicinity of the hybrid. Therefore, since none of them showed any more obvious evidence of *Q. lobata* ancestry than did the hybrid tree itself, the hypothesis that *Q. lobata* is one of the hybrid's parents was neither confirmed nor refuted by this progeny test.

In considering the origin of the hybrid, the most likely hypothesis, in my opinion, is that it was produced *in situ* from a direct cross between *Q. lobata,* probably as the pistillate parent, and *Q. turbinella californica,* as the pollen parent. This sympatric occurrence of the 2 at Live Oak Tank could have been as recent as 150 to 175 years ago, for the hybrid probably is best regarded as an F_1, and does not appear to be an exceptionally old tree.

Another possible, but much less probable, explanation is that the hybrid resulted from long-range pollination. Such an occurrence would have required a series of interrelated conditions including (Cottam, Tucker, and Drobnick, 1959; Tucker and Maze, 1966): 1, an overlap in the flowering times of *Q. lobata* at its southeastern limits and *Q. turbinella californica* at Live Oak Tank; 2, the occurrence, during the flowering period, of wind from the northwest or west sufficiently sustained to carry pollen the 150 or more miles between the two areas; 3, pollen sufficiently resistant to solar radiation to be capable of germinating after a wind-borne journey of several hours (Jaeger, 1961); 4, atmospheric phenomena which would cause some of the pollen to drift down at Live Oak Tank and settle precisely upon the minute stigmas of the flowers of *Q. turbinella californica* at a time of receptiveness. The probability of all these requirements having been met appears very low indeed. But even granting the *possibility,* it seems that such long-range pollination would stand much less chance of *effecting fertilization* than the pollen of *Q. turbinella californica,* which also would have been present, and in far greater abundance. Apparently, fertilization of a pistillate flower is better effected by pollen of its own species than by that of a foreign species, in cases where pollen of both is present. Whatever the basic physiological reason, the validity of this assumption may be inferred from the fact that hybrids between distantly related species of *Quercus,* as in the present instance, are rarely found in areas where both species are abundant. On the contrary (Palmer, 1948), they usually are found in areas where one species is abundant but the other is scarce, occurring only as infrequent, isolated individuals. Under such circumstances, it can be assumed that the rare species most probably is the female parent. Its chances of being pollinated by pollen of its own species would be extremely low, except for the limited possibility of self-pollination, whereas its chances of being pollinated by the abundant species would be very great.

In seeking an explanation to account for the occurrence of *Q. lobata* so far south and east of its main, continuous distribution, one cannot ignore the possibility of long-range transport, and inadvertent "planting" of an acorn of *Q. lobata* by Indians. The possibility appears rather remote, however. There seems to be no evidence that acorns were an item of barter between tribes of the Great Valley, or adjacent areas were *Q. lobata* flourished, and those as far east as Joshua Tree Monument (Sample, 1950). The area with which we are concerned, at least the vicinity of Twenty-nine Palms, was evidently territory of the Serrano (Kroeber, 1908, p. 33), a Shoshonean group centered in the San Bernardino Mountains. Although the statement has been made that "acorns were fairly abundant in the western part of Serrano territory, but the eastern bands got their supply from the western ones, or substituted other foods" (Kroeber, 1925, p. 618), such acorns would hardly have been those of *Q. lobata,* for this species probably did not occur in Serrano territory.

Kroeber's statement that "*Quercus lobata* was the species that the Cahuilla [a tribe of San Gorgonio Pass and the Colorado Desert] had most frequently accessible to them" (1925, p. 695) is evidently erroneous. From Barrows' very detailed survey of the plants utilized by the

Cahuilla, it is evident that they relied on species indigenous to their area (Barrows, 1900).

The most plausible hypothesis, in my judgment, is that *Q. lobata* had migrated southeastward at some period in the past, when climatic conditions were moister than at present. Subsequently, with a shift to drier conditions, the species was reduced in numbers, and finally eliminated altogether. First, however, it hybridized with the abundant and more drought-adapted *Q. turbinella californica* to produce the hybrid tree at Live Oak Tank.

The pluvial periods of the Pleistocene could have provided the opportunity for such a southeastward migration. However, it should be kept in mind that the last such period, the Wisconsin, was followed by a period of several thousand years that was warmer, and possibly drier, than the present. It seems likely that during this Post-Wisconsin Altithermal (Antevs, 1955) or Hypsithermal Interval (Deevey and Flint, 1957), the range of *Q. lobata* would have extended no farther southeastward than it does today, and probably not so far. Thus, its southeastward migration to the area of Live Oak Tank probably occurred after the Hypsithermal, during a period when the climate of southern California was wetter than at present.

Evidence from tree-ring analyses leaves little doubt that there have been marked climatic fluctuations in the western United States within the last several millennia. Schulman (1956) has noted that long-term shifts to wetter or to drier conditions were typical in southern California for a number of centuries preceding the mid-1600's (although these gave way to swings of much shorter duration after that time). In our present phytogeographic problem, tree-ring evidence may well provide answers to some of the questions. Certainly, a tree-ring analysis of the hybrid would give the approximate date of the initial hybridization. Although a sizeable body of dendrochonological data is at hand for the Southwest, comparable information for southern California is, as yet, very scanty. In future years, however, when many more tree-ring chronologies have been worked out for southern California such as that by Schulman (1947) for big-cone spruce, we will be nearer a solution to what, for the present, remains an intriguing riddle.

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NOTES AND NEWS

Confusion in Authorship of Stemodia verticillata Hassler.—In 1964 I collected a small, weedy member of the Scrophulariaceae in a pasture at Horneman's Ranch ("Bella Vista") about 4 miles north of Bahia Academy, Isla Santa Cruz (Indifatigalbe I.), El Archipielago de Colon (Galapagos I.), Ecuador.

While trying to identify this material, I found that it keyed to *Stemodia verticillata* (Mill.) Sprague, in Standley's *Flora of Costa Rica* (Fieldiana, Bot. 18:1111. 1938). A check of the Gray Herbarium Card Index revealed that this combination had been made twice prior to the publication of Sprague's paper (Bull. Misc. Inform. 1921:205–212. 1921). In each of the three cases, *Erinus verticillatus Mill.* (Gard. Dict. ed. 8, no. 5. 1768) was the basionym, so there is no doubt that each author was dealing with the same entity.

In 1909 Hassler (Trab. Mus. Farm. Fac. Ci. Med. Buenos Aires 21:110. 1909) published the transfer of *verticillatus* from *Erinus* to *Stemodia,* displacing the later *S. parviflora* Ait. Owing to the restricted circulation of this publication, Hassler's combination was overlooked and Boldringh again made the transfer (Zakfl. Landbouwstr. Java 165. 1916). In 1921 Sprague, failing to find the earlier papers, published *Stemodia verticillata* as a new combination for the third time.

Therefore, this weedy herb, which is wdely distributed in the American tropics and has been introduced elsewhere, together with its applicable synonymy, should be listed as follows:

Stemodia verticillata (Mill.) Hassler, Trab. Mus. Farm. Fac. Ci. Med. Buenos Aires 21:110. 1909. *Erinus verticillatus* Mill., Gard. ed. 8, no. 5. 1768. *Capraria humilis* Ait., Hort. Kew. ed. 1. 2:354. 1789. *Stemodia parviflora* Ait., Hort. Kew. ed. 2. 4:52. 1812. *Stemodia arenaria* H. B. K., Nov. Gen. Spec. 2:357. t. 175. 1817. *Conobea pumila* Spreng. Nov. Prov. 13. 1819. *Stemodia verticillata* (Mill.) Boldr., Zakfl. Landbouwstr. Java 165. 1916. *Stemodia verticillata* (Mill.) Sprague, Bull. Misc. Inform. 1921:211. 1921.—Ira L. Wiggins, Dudley Herbarium, Stanford University.